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NOTES ON SOUTH AFRICAN LARVAL TREMATODES *

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In previous publications (Faust 1919, 1920, 1920a) I have presented my studies on Cawston's South African larval flukes, have described methods for differentiating these one from the other and have indicated their bearing on life-history problems. Through a grant from the Streatfield Research Fund of the Royal College of Physicians and Surgeons of London, Dr. F. G. Cawston has been enabled to make collections of material which it has been my privilege to study. I desire, therefore, to acknowledge my indebtedness to Dr. Cawston for the opportunity afforded. The present study is published in order to aid in certain life-history studies now being carried on by several investigators in South Africa, as well as to make the data a matter of record.

Cercaria octadena nov. spec. (Fig. 1)

This new form was found in the digestive gland of *Physopsis africana,* collected at Sydenham and at Pinetown. In previous collections from this host at Sydenham, I did not find this furcocercous cercaria. It is one which might readily be confused with the two human schistosome cercariae which I have previously described from this region. It differs, however, in several important points.

In the first place the integument of both body and tail is free from spines. Secondly, the number and disposition of the so-called "mucin glands" differ from those of the two human species. In *C. octadena* there are two pairs of acidophilic glands and two pairs of basophilic glands, the latter being situated anteriorly to the former. These specific differences allow of no uncertainty as to the validity of the species. The worm has a body measurement of 170 by 60μ, while the unforked portion of the tail measures 180 by 40μ and the furci are 85μ long. The parthenita is a sporocyst.

Cawston (1920) has recently raised the question as to whether the cercaria which I described as the larva of *Schistosoma mansoni* might not be in reality that of *S. bovis,* inasmuch as he has not encountered *S. mansoni* clinically and the later species has been described for the locality. In this query Cawston overlooks the fact that the larva which I have described for South Africa as the cercaria of *Schistosoma mansoni* corresponds in all critical points with that also described from

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Venezuela (Faust 1919: 166), known experimentally to be the larva of *Schistosoma mansoni*. Furthermore, I have actually seen the lateral-spined eggs of *S. mansoni* preserved in the liver gland of *Physopsis africana* which Dr. Cawston collected from Ottawa, Natal, and later sent me. I am certain from my studies, therefore, that both species in question exist in Natal, and that there is a genetic relation between *Cercaria schistosomatis-mansoni* Faust of Natal and the adult *S. mansoni.*

It does seem highly probable, however, that *Cercaria octadena* is the larva of *Schistosoma bovis*. The general appearance as well as the specific characters of the cercaria indicate that it belongs to the group of mammalian schistosomes, while the presence of bovine schistosomiasis in Natal strengthens the probability. Difficulty in actually demonstrating the point lies in the fact that its occurrence thus far has been in mixed infections, along with the larvae of *S. haematobium* and *S. mansoni,* although this difficulty may be obviated by diagnosing both larvae and adults in experimental infection.

Cercaria secobii Cawston 1915 (Fig. 2)

Well-preserved material of *Cercaria secobii* secured from *Physopsis africana* at Pinetown and at Duff's Road, and from Sarnia sp. from the Umbibo River makes it possible to supplement the scant description of this species which I was obliged to give in a previous paper (Faust 1919: 165). Details of the digestive ceca have not been worked out, but there is a minute muscular pharynx behind the well-developed oral sucker. The acetabulum is small. Four pairs of mucin glands in tandem arrangement occupy the middle third of the body. They are neutrophilic in reaction. As is usual for the group their ducts open anteriad, laterad to the buccal cavity. A firm clump of germ-gland cells lies in the region midway between acetabulum and distal portion of the body proper. The entire larva is covered with spines.

Cercaria oblonga nov. spec. (Fig. 3)

This eye-spotted cercaria was secured from the digestive gland of *Tiara tuberculata* collected at Mt. Prospect. The body is oblong-ovate in contour, with a length measurement of 180μ and a width measurement of 65μ. The tail has a plump aspect at its proximal end but tapers out to a conspicuously pointed tip. It is almost twice as long as the body. The body and tail are both without integumentary spines. On the dorsal surface just anterior to the pharynx is a pair of eyespots with optic openings postero-laterad. Likewise, there is considerable pigmentation in the region of the cerebral commissure and over the dorsal and ventral nerve trunks. The oral sucker has a width of 30μ, with a small buccal cavity. The acetabulum is not well defined. It is probably represented by a glandular complex along the midline somewhat behind the middle of the body.

A long prepharynx leads into a small muscular pharynx. Behind this organ a short esophagus leads into ceca which have been entirely modified into discrete unicellular glands, there being perhaps thirty to forty in each cecal region. While they are morphologically and ontologically different from mucin glands their reaction to dyes leads one to believe they have the same physiological function.

The excretory bladder is a large vesicular structure which opens postero-dorsad through an attenuated duct. Absence of germ glands shows that the larvae is late in maturing. The redia in which the worm develops has a long muscular pharyngeal region but a very small cecum. The birthpore is also inconspicuous.

Cercaria puerilis nov. spec. (Fig. 4)

This minute stylet larva was secured from the digestive gland of *Tiara tuberculata* at Mt. Prospect. It has an ovoid body 80μ long, 53μ wide, and is as thick as wide. The tail is slightly longer than the body. No spines have been found on the integument. The stylet has a delicate piercing tip, a narrow shank and a blunt base. The oral sucker has a diameter of 22μ while the acetabulum measures only one-fourth that amount.

The oral atrium leads directly into a rotund pharynx behind which is found a typical digestive tract. It is lined with a few large epithelial cells. Three large mucin glands on each side of the ceca occupy a good share of the space anterior to the acetabulum. They give an acidophilic reaction and contain prominent granules. A large oval mass just to the left of the acetabulum constitutes the reproductive cell group. The excretory bladder is vesicular. The large cornua arise from it at angles of 120°. The worm develops in a sporocyst. Encystment takes place within a thin chitinous membrane, which is resistant to acids.

Cercaria ingracilis nov. spec. (Fig. 5)

The species is a xiphidiocercaria with a body covered with minute spines and a minute lenticular stylet. The tail is aspinose. The body measures 280 by 170μ and the tail 420μ long. Judging by its shape the movement of the larva is slow and awkward. The specimens were secured from the digestive gland of *Isidora schakoi* collected at Mt. Prospect.

The oral sucker of the worm has a transverse diameter of 54μ, while the acetabulum is slightly smaller. A long prepharyngeal region leads into a relatively large pharynx. Behind this organ a short esophagus opens into long narrow ceca extending to the subdistal region of the body. The epithelium of the gut is glandular. Outside of the cecal area are masses of granular mucin glands extending all the way from the oral sucker to the midacetabular region. Ducts of these glands empty laterad to the stylet. The excretory bladder is an irregular polygon with small collecting tubules leading from anteriad into the cornua. The excretory pore opens only slightly dorsad to posteriad. The genital cells consist of an irregular-shaped mass dorsal to the acetabulum and extending somewhat anteriad. The parthenita is a sporocyst. Encystment has not been observed.

Cercaria cephaladena nov. spec. (Fig. 6)

Cercaria cephaladena is a stylet larva with very delicately-formed organs. It was obtained from the digestive glands of *Isidora schakoi* at Mt. Prospect. The body is covered with delicate spines, while the tail is aspinose. The stylet is regularly quill-shaped. The body measures 210 by 75μ and the tail 175μ in length. The oral sucker has a transverse diameter of 22μ and the acetabulum 25μ. Leading in from the oral atrium is an elongate pyriform pharynx which opens almost directly into the digestive ceca. These latter are slender tubes extending to the subdistal region of the body. The mucin glands lie in the cephalic area of the worm. They consist of five pairs of basophilic glands with small compact nuclei. The excretory bladder consists of a median vesicular portion which opens posteriad through a slender tube, and an anterior portion lined with glandular epithelium.

The most unique system is the genital complex. It is far advanced for a larva although none of the parts are yet mature. The testes have become separated as distinct spherical masses lying tangentially posterior to the ootype. Prostate and cirrus organs are distinguishable. The vitellaria consist of small masses extending from the pharyngeal region to the line of the posterior testis. Definite vitelline ducts extend transversely to the ootype. These structures taken together clearly distinguish this larva as a plagiorchiine species.

Cercaria humilis nov. spec. (Fig. 7)

This xiphidiocercaria was secured from the digestive gland of *Lymnaea natalensis* at Mt. Prospect and from *L. natalensis* and *Physopsis africana* at Duff's Road. It has a body measurement of 200 by 70μ, and a tail 118μ long. Body and tail are aspinose. The oral sucker has a transverse diameter of 43μ while the smaller ventral sucker is only 29μ in diameter. A long prepharynx leads from the oval cavity to the compact spherical pharynx, which latter organ is 12μ in diameter. Behind this a long slender esophagus bifurcates just in front of the acetabulum to form the ceca. The latter organs extend to the subdistal margin of the body. There are about thirteen pairs of mucin glands in the body, consisting of nine pairs of granular acidophilic cells lying posteriad and four pairs of *mucoid basophilic cells* situated anteriad. The ducts of these glands are associated in compact bundles. The openings of the ducts near the stylet are small in diameter and close together. The excretory bladder proper is beet-shaped, with cornua arising just laterad from the median line. The pore is dorsoposteriad. The genital cell mass is an irregular structure lying below the sinistral margin of the acetabulum. The parthenita is a sporocyst. Encystment has not been observed.

This larva resembles *Cercaria cawstoni* in certain respects, particularly the type of digestive tract, but differs with respect to kind and number of mucin glands, the stylet, the excretory bladder and the genital complex. These differences in a larval trematode denote a very considerable difference in adult structure, more profound, indeed, than that distinguishing two somewhat related species.

Cercaria vertebraeformis nov. spec. (Fig. 8)

Cercaria vertebraeformis is a large worm exhibiting many points of interest in the morphology of the trematodes. The body is ovate-elongate, while the heavy muscular tail has both a dorsal and a ventral fluted keel. Neither body nor tail possess spines and no stylet has been found. The body measures 270 by 125μ while the tail has a length measurement of 290μ. Oral sucker and acetabulum are equally large, with a longitudinal diameter of 58μ. The transverse diameter is slightly less.

Within the oral atrium is a prepharyngeal region. The pharynx (25μ in diameter) leads into an esophagus impregnated with chitin which has grown in from the orifice and extends inward slightly beyond the forking of the gut. At this point arise true digestive ceca which extend posteriad somewhat beyond the limits of the acetabulum. These ceca are composed of a single layer of epithelium which consists of a syncytial mass of cells. The mucin glands are located laterad to the excretory bladder. A group of about sixteen small polygonal cells with minute nuclei and cytoplasmic strands radiating from the nucleus to the periphery of the cell have their outlets through a conspicuous bundle of ducts that is ovoid with an anterior extension like a truncated pyramid, the lateral angles of which run out into relatively small collecting tubes. The excretory pore is posterodorsad. The genital cell complex consists of an irregular-shaped mass with three arms lying dorsad to the acetabulum. The posterior end of the body has an integumentary thickening giving a mucoid reaction. The sporocyst is sausage-shaped and has numerous constrictions in its outline Encystment has not been observed.

Cercaria macrura nov. spec. (Figs. 9-13)

This unique larva was found in the digestive gland of *Planorbis pfefferi* at Merebank and Mayville. It develops in a large redia with small pharynx, tortuous gut and no "feet." Very few of the features of the body of this worm are sufficiently developed during the cercarial stage to differentiate the fluke *per se* but the caudal appendages are clearly defined.

As the cercaria develops from the germ ball three regions are distinguishable (Fig. 9), an elongate portion which is to develop into the body proper, a cordate portion which is to constitute the main caudal region and a lateral finger-like process which will grow into the caudal cecum. As growth takes place (Fig. 10) the body portion becomes elongate club-shaped. Within the tail a dense ball of glandular cells becomes noticeable, while the caudal cecum, consisting of a column of single cells, becomes hollowed out. In view of the excretory function of the caudal cecum in a related species, Cort and Nichols (1920: 10) have designated it the excretory projection. The opening extends from the distal end of the cecum directly through to the distal margin of the caudal trunk. Later (Fig. 11), the latter region becomes considerably enlarged, the glands become granular with vesicular inclusions and the margins become elytral. At this stage the caudal cecum begins to decrease in size while the body and tail trunk are of maximum size. The body has a length measurement of 180μ and a frontal diameter of 30μ. The oral sucker is 28μ in transection and the acetabulum of equal size. The small pharynx measures 18μ in section. A typically forking digestive tract is visible. Mucin glands and genital complex have not yet developed while the excretory system cannot be made out. The caudal trunk has a gross length of 160μ and a gross width of 100μ. The connection between this region and the outside has now become closed at the distal margin.

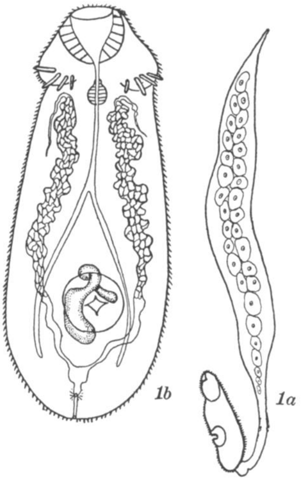
The next stage (Fig. 12) shows a distinct tendency toward encystment. The glands have been utilized in the formation of a cyst membrane on the inner surface of the caudal trunk while the body of the worm becomes invaginated into the cyst cavity provided. The elytra become resorbed. The caudal cecum persists. Later (Fig. 13), the worm has become entirely engulfed within its own tail trunk, while the caudal cecum acts as a stipe for attachment to objects near at hand. In this way a larva, ontogenetically young and with only slight differentiation, passes into the encysted stage (agamodistome). Such a condition would not be possible at this stage in a larva depending on the development of cystogenous glands within itself.

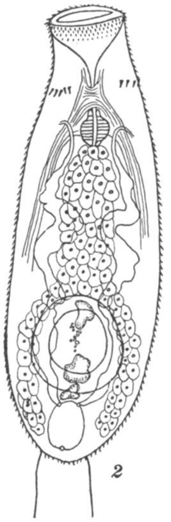
The position of *Cercaria macrura* is difficult to define. It has some features in common with the rhopalocercous larvae, although the fact that the tail is actually used as an organ of protection and encystment places it in the *cystophorous* group. The mechanism for encystment makes possible the transfer to a second intermediate host which in the case of a related species, *C. cystophora,* is the dragon-fly, *Colopteryx virgo.*

Cercaria caudadena nov. spec. (Text figs. 1a, 1b)

This larva was obtained from the digestive gland of *Planorbis pfefferi* collected at Merebank. From its tail it might be regarded as a megalocercous larva but the body clearly defines it as an echinostome cercaria.

The body of *Cercaria caudadena* is oblong-ovate with a distinct coronal constriction, in which region there is a circlet of not more than twenty-four relatively large spines in a single series. The body is entirely covered with minute spines. The tail is aspinose and is several times the length of the body and almost twice the width. The oral sucker has a transverse diameter of 38μ while the acetabulum, situated in the posterior third of the body, is of equal transection.





Text figs. 1a, 1b.—*Cercaria caudadena: 1a,* lateral view of entire larva, × 50; *1b,* ventral view of body, × 233.

Text fig. 2.—*Cercaria cucumeriformis,* ventral view of body and proximal portion of tail, × 233.

The dilated oral cavity of the larva becomes constricted as it reaches the region of the pharynx. The latter organ has a transverse diameter of 12μ and lies in the plane of the coronal constriction. A long narrow esophagus runs posteriad, forking half way toward the acetabulum and merging into ceca which extend somewhat beyond the posterior margin of the acetabulum. Granular mucin glands extend from the region of the pharynx to the acetabulum, filling most of the intermediate space. The excretory bladder is roughly triangular with a narrow tube running caudad and opening through a small pore dorsad. From the anterolateral extensions of the bladder irregular ducts arise, which are enlarged between the acetabulum and pharynx to accommodate the rough crystalloid deposits of the system. The ducts are reflexed in the region near the pharynx in a typical echinostome fashion. The genital complex consists of a mass coiled upon itself in the region of the acetabulum. The tail has a core of large glandular cells of unknown function. The parthenita is a redia with typical pharynx, gut and "feet." Encystment has not been observed.

Cercaria cucumeriformis nov. spec. (Text fig. 2)

Cercaria cucumeriformis is an echinostome larva specifically different from others of this group described from South Africa in that the oral sucker is directed forward instead of ventrad or antero-ventrad. The cercaria was found in the digestive gland of *Isidora schakoi* at Merebank and in *Lymnaea natalensis* taken from the Umgeni River.

The body of the worm is elongate with the anterior end truncate and the posterior end rotund. The body measures 260μ long by 83μ at the greatest transverse diameter. The tail is slightly longer than the body. The collar region is marked by a small number of coronal spines of spiculate type. The oral sucker measures 43μ in transection and the acetabulum, situated far caudad, measures 50μ in diameter.

From the oral cavity the prepharynx leads into a large muscular pharynx behind which is an esophageal region. The ceca arise just anterior to the acetabulum and continue to the subdistal region of the body. Both esophagus and ceca are unique in consisting of glandular epithelium throughout their entire length. A cross section in the region of the esophagus shows from eight to eleven cells surrounding its lumen, but in the ceca the number in section is reduced to three or at most four. The excretory bladder is spheroidal, with pore posterodorsad, and collecting tubes that arise from the anterior wall some little distance from the midline. As they are traced forward they are seen to undulate, with irregular dilatations along the course. They become constricted, however, in the region of the pharynx and turn back on themselves. The genital complex lies dorsal to the acetabulum. There are three large cells, but no definite differentiation has been noted. The parthenita is a redia with no conspicuous characters. Encystment has not been found.

Cercaria catenata Cawston 1917

I have found *C. catenata* in *Isidora schakoi* collected at Merebank.

Cercaria pigmentosa Cawston 1919

C. pigmentosa was found in *Lymnaea natalensis* collected at Sydenham and in *Physopsis africana* at Duff's Road. This larva is undoubtedly the cercaria of a Fasciola, but while both *F. hepatica* and *F. gigantica* occur in South Africa I have been able to demonstrate only the one species of larva.

DISCUSSION

This paper presents ten new species of South African cercariae in addition to clearing up the details of structure in *Cercaria secobii* and giving new distribution records for two other species. There is thus constituted a group of 25 well-defined larval trematodes with the following distribution: amphistome, 1; monostome, 1; echinostome, 7; xiphidiocercariae, 5; furcocercariae, 7; gymnocephalous cercariae, 2; cystophorous cercaria, 1; allocreadine cercaria, 1. I have had an opportunity to study material from all of these species except *Cercaria coma* Gilchrist 1918. In some instances as many as ten or twelve separate collections of one species have been available for use. Since no opportunity was afforded for working on the living material I have had to determine, therefore, (1) what reagent is the most reliable for diagnostic work in this group, (2) which organs are the least distorted by preservation, and likewise, (3) which organs can be depended on in preserved material for specific diagnosis.

With respect to the first query, fixatives containing acid are not successful for long-distance carriage, while five per cent formalin proves eminently satisfactory. Formalin hardens the tissues sufficiently to prevent maceration in carriage and at the same time make the material especially fitted for the study of toto mounts. There is no vagueness of differentiation such as is commonly found in the formalin preservation of large mammalian organs.

A comparison between the study of living and preserved larval trematodes consists primarily in the fact that the living flukes permit a study of movement and of the flame-cells, which the preserved material does not, whereas the preserved material frequently gives a clearer picture of the germ-cell complex. Usually the excretory bladder and the primary collecting tubules are likewise more conspicuous in the living specimens, while the digestive system, including mucin glands, is more clearly depicted in stained mounts. If it were possible, therefore, to study an abundance of living material the excretory system offers a definite basis for diagnosis and differentiation. But this opportunity is frequently not afforded, so that it is even more important that a conservative system be found which permits diagnosis in preserved specimens. The gross external anatomy is obviously not to be considered, and the digestive tract *sensu stricto* is often not specific. The genital complex is not always dependable, due to the fact that it frequently develops late in the ontogeny of the worm. On the other hand, a study of South African as well as many other species leads me to believe that the mucin glands offer a system highly differentiated within a particular group, yet constant within the species. It is almost entirely on this basis that a differential diagnosis has been made among the three species of human schistosome cercariae and it is this system that offers in this study the differentiation between these three schistosome species and *Cercaria octadena,* the probable larva of *Schistosoma bovis.*

The fact that certain of these glands constantly have a basophilic reaction (and can be readily differentiated by Best's carmine stain as well as hematoxylin stains) and that others are acidophilic in reaction, not only makes the differentiation easier but presents a most important problem in connection with the physiology of the larva and the pathology of the host. In this connection it may be mentioned that the differentiation of these two varieties of digestive glands has made the term mucin gland untenable when applied to these glands as a whole. I wish to suggest, therefore, that the term *cephalic gland* (Cort 1919: 501) be used in place of mucin gland, so that one may refer to basophilic, neutrophilic or acidophilic glands of this type without confusion or misinterpretation. A comparative study of the effects of these glands on host tissues indicates that basophilic and acidophilic glands are complementary in function and that a larva possessing the two differentiated types can penetrate the host much more effectively than one possessing only one type. The schistosome cercariae are notable examples of the dimorphic type of staining reaction.

Leiper (1915: 188) has found some twenty-five species of cercariae in his study of the schistosome problem in Egypt. While the larvae of *Schistosoma haematobium* and of *S. mansoni* occur in both Egypt and Natal, the other described cercariae are specifically different. It seems quite probable that several of the species reported for Egypt are present in South Africa but have not yet been collected, as for example the larval amphistomes *Cercaria pigmentata* and *C. aegyptiaci,* the adult forms of which have been reported for Natal. It is less likely that some of the larval flukes first described from South Africa will be found in Egypt, since the latter country has been extensively surveyed for trematodes. A collection of material from tropical West Africa would undoubtedly yield important data in connection with the two areas now relatively well surveyed.

SUMMARY

1. Further collections of larval trematodes from South Africa have made possible the description of ten new species.

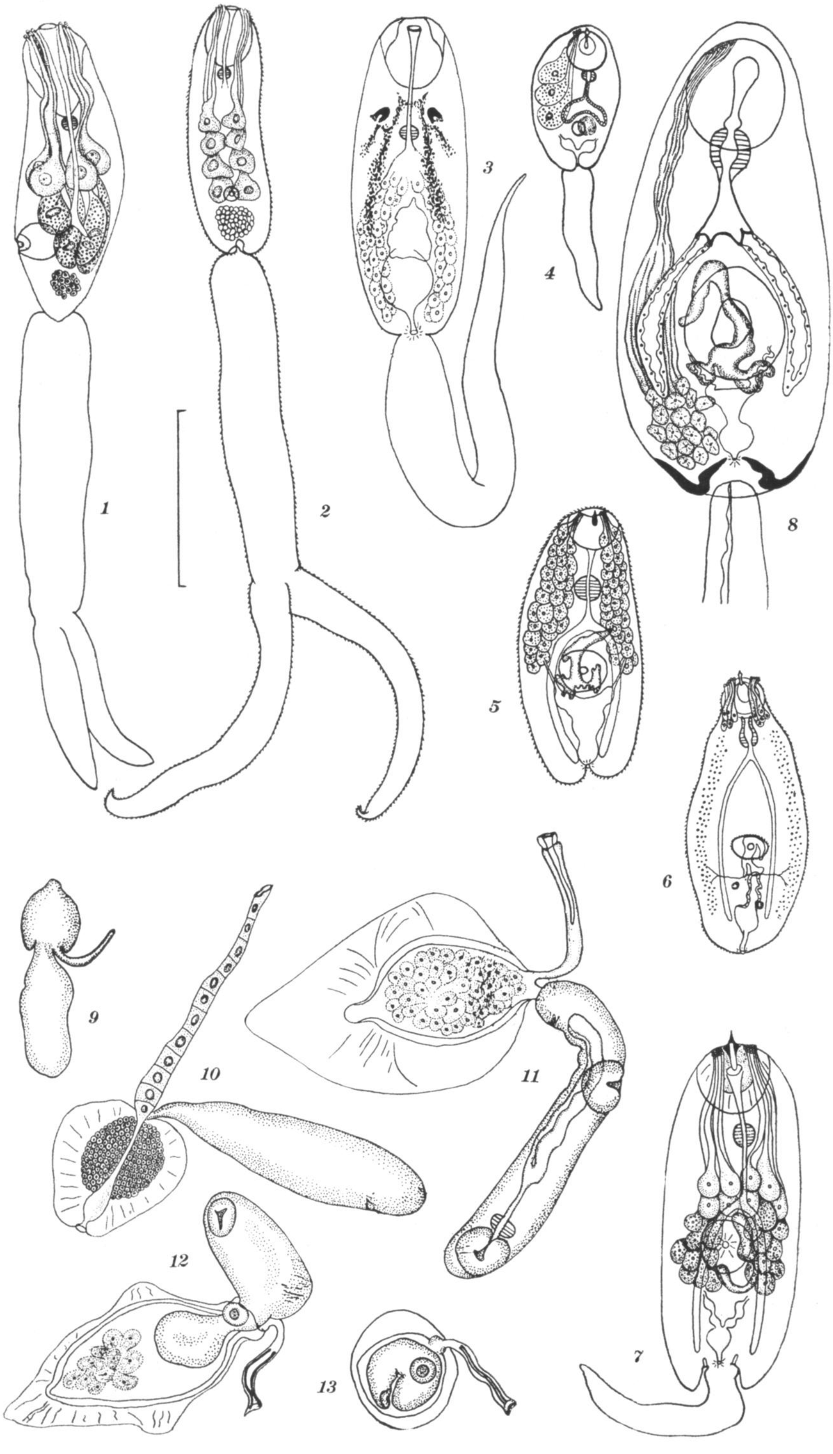


PLATE III

2. *Cercaria octadena,* the probable larva of *Schistosoma bovis,* is readily differentiated from the larval stages of the two human schistosomes in South Africa on the basis of its digestive glands.

3. The digestive glands are the most important structures for differentiating preserved material.

4. Since the term mucin gland is applicable only to the digestive gland giving a basophilic reaction the term *cephalic gland* (Cort) is suggested to designate all such glands, including those giving basophilic, neutrophilic and acidophilic reactions.

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EXPLANATION OF PLATE III

Fig. 1.—Lateral view of *Cercaria octadena.*
Fig. 2.—Ventral view of *C. secobii.*
Fig. 3.—Ventral view of *C. oblonga.*
Fig. 4.—Ventral view of *C. puerilis.*
Fig. 5.—Ventral view of *C. ingracilis.*
Fig. 6.—Ventral view of *C. cephaladena.*
Fig. 7.—Ventral view of *C. humilis.*
Fig. 8.—Ventral view of *C. vertabraeformis.*
Figs. 9-13.—Progressive stages in the development of *C. macrura.*

Note.—The line has a value of 0.1 mm. in all figures except fig. 5, where it has a value of 0.18 mm.